

Sacoglossan Opisthobranchs on Northwestern Pacific Shores: *Stiliger berghi* Baba, 1937, and *Elysia* sp. on Filamentous Red Algae

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Abstract. At least 20 species of sacoglossan opisthobranchs worldwide feed on delicately branching red algae; these species include members of three genera (*Hermaea* Lovén, 1844; *Stiliger* Ehrenbergh, 1831; and *Elysia* Risso, 1818) in three sacoglossan families. The algal hosts include members of three algal families and at least ten algal genera in the order Ceramiales. We studied two sacoglossan species that feed on filamentous red algae: (1) the temperate to boreal *Stiliger berghi* Baba, 1937, on wave-sheltered shores of Honshu and Hokkaido, Japan, and (2) the subtropical to tropical *Elysia* sp. on moderately wave-exposed shores of Okinawajima and Honshu, Japan. Preference experiments demonstrated that *S. berghi* prefers to associate with the alga *Dasya* when given pairwise algal choices but readily consumes members of several algal genera and exhibits no preferences between algal life-history phases (diploid tetrasporophytes vs. haploid female gametophytes). *Elysia* sp. is a small sacoglossan that consumes uniseriate and polysiphonous red algae. Given the small size and seasonally abundant populations of organisms that feed on red algae, we predict that these sacoglossans and their ecological analogs on other shores may have an unexpectedly important role in consuming and/or fragmenting ceramialean red algae. Given the known propensity of these algae to be dispersed by international shipping and oyster mariculture, careful malacological consideration should be given to the potential of sacoglossans to be inadvertent “hitchhikers” on a global scale.

INTRODUCTION

Marine red algae have been extensively introduced around the world by the fouling of ship hulls, the transport and relaying of oysters, and the introduction of epiphytized host plants. Of the macroalgae currently recognized as introduced (reviewed by Trowbridge, 2006), members of the red algal order Ceramiales predominate. The dramatic proliferation of nonindigenous red algae (e.g., *Womersleyella setacea* covering the benthos in the Mediterranean and “*Heterosiphonia japonica*” on Atlantic European shores) is widely recognized among phycologists and invasion biologists but not among malacologists. The role of herbivory, particularly by sacoglossans, in controlling and/or exacerbating the spread of red algae has been long

overlooked. Furthermore, surprisingly little malacological attention has been focused on the possibility that many of the newly reported *Hermaea* spp. may not be indigenous to the regions from which they have been described.

The taxonomy and ecology of these specialized herbivores on native and introduced ceramialean hosts in different areas of the world merits investigation. Throughout temperate and tropical areas of the world, there are numerous sacoglossan opisthobranchs that feed on species of Ceramiales; these sacoglossans belong to at least three sacoglossan families and three genera: *Hermaea* Lovén, 1844; *Stiliger* Ehrenbergh, 1831; and *Elysia* Risso, 1818 (Table 1).

Our objectives of this report are threefold: (1) to review and compare the sacoglossan opisthobranchs on ceramialean red algae worldwide, (2) to evaluate the similarities and differences of the algal hosts, and (3) to describe the reproductive features and feeding ecology

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Table 1

List of sacoglossan opisthobranchs that actually or potentially consume filamentous red algae. An em dash (—) denotes no data; “NA” denotes that this reference was not available to the authors.

Region	Sacoglossan species	Algal hosts	Maximum body length (mm)	Diameter of uncleaved ova (µm)	Number of ova per capsule	Diameter of capsules (µm)	Larval shell*	References
Australian	<i>Elysia</i> cf. <i>furvacauda</i>	<i>Codium</i> , <i>Microdictyon</i> , and red algae**	ca. 7	—	—	—	—	Brandley (1984)
Australian	<i>Hermæa evelinæmarcusæ</i> Jensen, 1993	<i>Griffithsia</i>	2	—	—	95.3 × 122.6	—	Jensen (1993)
NE Atlantic	<i>Elysia viridis</i> (Montagu, 1804)	<i>Codium</i> , <i>Bryopsis</i> , <i>Chaetomorpha</i> , <i>Cladophora</i> , <i>Acetabularia?</i> , <i>Griffithsia</i> , <i>Halurus</i> , <i>Dasya</i> , <i>Dasydiphonia</i>	70	60–76	1–2	85–135 × 100–180 (if single ovum; larger if two ova)	Type 1	Thompson (1976); Schmekel & Portmann (1982); Jensen (2001); Van Bragt (2004); Trowbridge (unpubl. data); R. Dekker (pers. comm.)
NE Atlantic	<i>Hermæa bifida</i> (Montagu, 1815)	<i>Griffithsia</i> , <i>Halurus</i> , <i>Bornetia</i> , <i>Heterosiphonia</i> , <i>Dasydiphonia</i> , [<i>Delesseria</i>]***	23	49–54, 48	1–2	94–103 × 112–129, 104 × 128	Type 1	Wright (1859); Robertson (1868); Duerden (1896); Miller (1958); Taylor (1971); Kremer & Schmitz (1976); Thompson (1976); Kremer (1977); Schmekel & Portmann (1982); Van Bragt (2004); Trowbridge (pers. obs.)
NE Atlantic	<i>Hermæa boucheti</i> Cervera et al., 1991	—	4.5	—	—	—	—	Cervera et al. (1991)
NE Atlantic	<i>Hermæa paucicirra</i> Pruvot-Fol, 1953	On <i>Codium fragile</i> (presumably on epiphytic red algae common on <i>C. fragile</i>)	3.5	ca. 30	—	60 × 100 (variable)	—	Salvat (1968); Cervera et al. (1991)
NE Atlantic	<i>Hermæa variopicta</i> (Costa, 1869)	<i>Halurus</i>	40	—	—	—	—	Lemeche & Thompson (1974); Thompson & Brown (1976); Gascoigne (1979); Schmekel & Portmann (1982)
NE Atlantic	<i>Hermæa ghanensis</i> Caballer, Ortea, & Moro, 2006	NA	NA	NA	NA	NA	NA	Caballer, Ortea, & Moro (2006)
NE Pacific	<i>Hermæa olivæ</i> (MacFarland, 1966)	<i>Polysiphonia</i> , <i>Griffithsia</i> , filamentous green algae?	11.4	—	1	—	—	MacFarland (1966); Trowbridge (2002); Behrens & Hermosillo (2005)

Table 1
Continued.

Region	Sacoglossan species	Algal hosts	Maximum body length (mm)	Diameter of uncleaved ova (µm)	Number of ova per capsule	Diameter of capsules (µm)	Larval shell*	References
NE Pacific	<i>Hermæa hillae</i> Marcus & Marcus, 1967	—	12	—	—	—	—	Trowbridge (2002)
NE Pacific	<i>Stiliger fuscovittatus</i> Lance, 1962	<i>Polysiphonia</i> , <i>Callithamnion</i> , & <i>Dasya</i>	15	66.5, 70–95	1 (or 2)	110–150	Type 1	Lance (1962); Case (1972); Clark & Busacca (1978); Strathmann (1987); Behrens & Hermosillo (2005); Lance (pers. comm. to CDT); Hansen (pers. comm. to CDT)
NW Atlantic	<i>Hermæa cruciata</i> Gould, 1870	<i>Dasya</i> , <i>Griffithsia</i> , [<i>Agardhiella</i>]***	10	77, ca. 100	1	ca. 150	—	Vogel (1971); Marcus (1972); Jensen (1983); Clark et al. (1990)
NW Atlantic	<i>Hermæa nautica</i> Caballer & Ortea, 2007	—	2	—	—	—	—	Caballer & Ortea (2007)
NW Pacific	<i>Elysia abeilamakusana</i> Baba, 1955	<i>Bryopsis</i> , <i>Chaetomorpha</i> , <i>Cladophora</i> , <i>Griffithsia</i>	20	—	—	—	—	Baba (1955), Hirano & Hirano (unpubl. obs.)
NW Pacific	<i>Hermæa noto</i> (Baba, 1959)	<i>Griffithsia</i>	10	—	—	—	—	Baba (1959); Nakano (2004); Ono (2004); Hirano & Hirano (unpubl. obs.)
NW Pacific	<i>Hermæa wrangeliae</i> (Ichikawa, 1993)	<i>Wrangelia</i>	10	—	—	—	—	Ichikawa (1993)
NW Pacific	<i>Hermæa zosteræ</i> (Baba, 1959)	— (Found on <i>Zostera marina</i>)	3	—	—	—	—	Baba (1959)
NW Pacific	<i>Stiliger bergii</i> Baba, 1937	<i>Polysiphonia</i> , <i>Dasya</i> , <i>Ceramium</i> , <i>Griffithsia</i> , [<i>Galaxaura</i>]***	10	ca. 65 66.5 62 × 68	1	ca. 100 × 130 104 × 136	Type 1	Baba (1937, 1959); Baba & Hamatani (1952); Hamatani (1960, 1963); this report
NW Pacific & Indo-Pacific?	<i>Elysia</i> sp.	Uniseriate and polysiphonous reds	8	ca. 100	1	ca. 200	Type 1	this report
SW Atlantic	<i>Hermæa coirala</i> Marcus, 1955	—	9	—	—	—	—	Marcus (1955)

* Type 1 shells, according to original authors.

** Epiphytic red algae (Order Ceramiales: *Spyridia*, *Centroceros*, *Ceramium*, and *Laurencia*; Order Acrochaetales: *Acrochaetium*), but which may be hosts were not investigated.

*** Unlikely algal host.

of two Japanese species (*Stiliger berghi* Baba, 1937, and *Elysia* sp.) to enhance future identification of these species and to stimulate additional records within the North Pacific region.

SACOGLOSSAN REVIEW

Within the genus *Hermaea*, the most abundant species (in terms of population density) is *Hermaea bifida* (Montagu, 1815); despite its frequency, the species' preference for native vs. introduced red algae on European shores has been overlooked. The uncommon to rare congeners include *H. variopicta* (Costa, 1869), which is considered by some authors to belong to genus *Hermaeopsis* A. Costa, 1869; *H. paucicirra* Pruvot-Fol, 1953, on NE Atlantic shores; *H. cruciata* Gould, 1870, on NW Atlantic shores; *H. oliviae* (MacFarland, 1966) and *H. hillae* Marcus & Marcus, 1967, on NE Pacific shores; *H. wrangeliae* (Ichikawa, 1993) on NW Pacific shores; *H. noto* (Baba, 1959) on NW Pacific shores; and *H. evelinemarkusae* Jensen, 1993, on Australian shores. [Note that Ichikawa reported her species as *Aplysiopsis wrangeliae*, but that genus contains only green-algal feeders, not red-algal ones; *A. oliviae* was moved into *Hermaea* (Rudman, 2000, with a 2001 update; Behrens & Hermosillo, 2005), based largely on diet. The first author (CDT) considers *A. wrangeliae* to belong to the genus *Hermaea*, though the absence of a voucher and the lack of descriptions of radular teeth and the reproductive system hinders confirmation of the genus.] Numerous additional *Hermaea* spp. have been recorded: *H. boucheti* Cervera et al., 1991 (now considered to be *H. bifida* by Cervera et al., 2004), and *H. ghanensis* Caballer et al., 2006, on NE Atlantic shores; *H. nautica* Caballer et al., 2007, on NW Atlantic shores; *H. coirala* Marcus, 1955, on SW Atlantic shores (considered to be conspecific with *H. cruciata* by many colleagues); *H. zosteriae* (Baba, 1959) on Japanese shores (considered to be conspecific with *H. noto* by some colleagues; see Rudman, 2002); and congeners in the Indo-Pacific region and Southern Ocean (e.g., Carlson & Hoff, 2003; Burn, 2006; Sea Slug Forum, www.seaslugforum.net). These species are often assumed to feed on red algae, although observational evidence is still frequently lacking.

There are at least two *Stiliger* species that feed selectively on filamentous red algae: *Stiliger fuscovittatus* Lance, 1962, is an abundant, though insufficiently studied, sacoglossan on NE Pacific shores (Lance, 1962; Case, 1972; Trowbridge, 2002) and *S. berghi* Baba, 1937, on NW Pacific shores (Table 1). The NE Pacific specimens of *S. fuscovittatus* belong to the genus *Stiliger*, not to *Ercolania*: the teeth are blade-shaped, not sabot-shaped, and the species eats red algae, not green algae (characteristic of *Ercolania* spp.). [The true identity of "*Ercolania fuscovittata*" recorded from

Florida and the Gulf of Mexico is presently unclear, as the radular tooth shape has never been reported; see discussion on Sea Slug Forum]. The NW Pacific *S. berghi* was described from 15 specimens collected in 1935 from Tomioka, Amakusa, Japan (Baba, 1937); the species was subsequently reported from Osaka Bay, Inland Sea of Seto, and Toyama Bay (Inaba, 1958, 1962; Baba, 1959; Hamatani, 1961). This species has rarely been reported, presumably owing to its small size, cryptic coloration, and patchy distribution. It has not been included in any of the recent popular books on Japanese opisthobranchs (Suzuki, 2000; Nakano, 2004; Ono, 2004) or a recent Japanese sacoglossan account (Hamatani, 2000). The only literature report for this species outside of Japan is from Russian shores—Peter the Great Bay, Sea of Japan (Adrianov & Kussakin, 1998). Not only is there distributional uncertainty but there is also taxonomic uncertainty. Baba & Hamatani (1970, p. 202) suggested that *S. berghi* may "belong to another genus, not yet defined."

Finally, at least four *Elysia* spp. consume red algae (Table 1). *Elysia viridis* (Montagu, 1804) on European shores feeds not only on four genera of green algae but also on four genera of red algae, including native and introduced species. The Australian *Elysia* cf. *furva-cauda* consumes green algae in some months and unidentified red algal epiphytes during other times (Brandley, 1984). On Japanese shores, *Elysia abei* amakusana feeds on the red alga *Griffithsia* as well as on green algae (*Bryopsis*, *Cladophora*, *Chaetomorpha*, etc.; Y.J. Hirano & Y.M. Hirano, unpublished observations). Originally described as separate species, *E. abei* Baba, 1955, and *E. amakusana* Baba, 1955, are currently presumed to be conspecific by many malacologists (see www.seaslugforum.net). Finally, on Okinawan shores, there is a small *Elysia* sp. that feeds on uniseriate and polysiphonous filaments of red algae. One specimen of this species has also been collected from Shimoda, Izu Peninsula, Honshu. Our undescribed *Elysia* sp. may be conspecific with *Elysia* sp. 2 from Hachijo-jima, Honshu (Nakano, 2004), *Elysia* sp. 5 from the Ryukyu Islands (Ono, 2004), or an *Elysia* sp. in the Philippines (T.M. Gosliner, personal communication). Until the internal anatomy of these specimens has been characterized, we will limit our discussion to our *Elysia* sp.

ALGAL HOST REVIEW

All of the sacoglossans that associate with red algae use hosts within the order Ceramiales; there are no confirmed reports of hosts from other algal orders (Table 2). Intriguingly, the hosts belong to three algal families: the high-diversity Rhodomelaceae and Ceramiaceae as well as the comparatively lower-diversity Dasyaceae (Table 2). As these families are distinguished

Table 2

Classification of described hosts of sacoglossans that feed on red algae, based on currently recognized names in AlgaeBase (Guiry et al., 2006). The number of algal genera that are used as hosts are shown relative to the number of genera described in each algal family (based on Guiry et al., 2006).

Orders	Families	Number of genera	Genera	References
Ceramiales				
	Rhodomelaceae	1/137 (0.7%)	<i>Polysiphonia</i>	Baba (1937, 1959); MacFarland (1966); this report
	Dasyaceae	3/18 (16.7%)	<i>Dasya</i>	Van Bragt (2004); Lance (pers. comm. to CDT); Hansen (pers. comm. to CDT)
			<i>Dasysiphonia</i>	Van Bragt (2004)
			<i>Heterosiphonia</i>	Thompson (1976)
	Ceramiceae	6/142 (4.2%)	<i>Ceramium</i>	this report
			<i>Griffithsia</i>	Robertson (1868) ¹ ; Trowbridge (unpubl. obs.); this report
			<i>Halurus</i>	Wright (1859) ² ; Duerden (1896); Miller (1958) ³ ; Kremer & Schmitz (1976) ³ ; Trowbridge (unpubl. obs.) ³
			<i>Bornetia</i>	Cornet & Marche-Marchad (1951)
			<i>Wrangelia</i>	Ichikawa (1993)
			<i>Callithamnion</i>	Lance (1962), Trowbridge (2002)

¹*G. corallina* is considered to be *G. corallinoides*. ²*G. setacea* and ³*G. flosculosa* are considered to be *Halurus flosculosus*.

primarily on reproductive attributes, what determines which families and genera within these families are appropriate hosts for sacoglossans? All host genera are either monosiphonous (with a single row of cells attached end-to-end) or polysiphonous (with a central series of cells surrounded by pericentral cells of identical height) with large cells. Polysiphonous hosts are frequently assigned to the genus *Polysiphonia* (Tables 1 and 2). However, given that the taxonomic status of the high-diversity genus has been historically in constant flux and was recently subdivided into multiple polysiphonous clades (e.g., *Womersleyella*, *Neosiphonia*, *Polysiphonia*, etc.; see Choi et al., 2001), the number of polysiphonous host genera recognized by malacologists is undoubtedly an underestimate. Cortication—the covering of the algal axis with a layer of small cells—occurs in a few host genera (e.g., *Ceramium*, *Dasya*), but most host genera lack cortication. *Ceramium* exhibits regions of cortication and regions without, thus providing sacoglossans access to small cells and large cells, respectively. Some genera, such as *Dasya*, have highly corticated main axes but monosiphonous branchlets. What is not clear, however, is why many red-algal genera, with seemingly appropriate morphology for sacoglossan feeding, are not reported as hosts. To what extent are the results in Table 2 a reflection of actual host use versus an artifact of challenging phycological identifications by malacologists? We predict that future collaboration between sacoglossan researchers and taxonomists of red algae will reveal substantially greater host diversity than is currently recognized.

METHODS

Study regions: The present investigation was conducted primarily at three regions in Japan: (1) the Oshoro

Marine Station, Hokkaido University; (2) the Misaki Marine Biological Station (MMBS), on the Miura Peninsula, Honshu, University of Tokyo; and (3) Okinawajima, the main island of Okinawa. The Oshoro Marine Station is on the southwestern side of Hokkaido on the Sea of Japan (Figure 1A); collections were made at several sites within the wave-sheltered bay. MMBS is on the Sagami Bay shores of the Miura Peninsula on the Pacific coast of Honshu; collections were made from Araiama and Moroiso Bay at MMBS (Figure 1B). Finally, we collected sacoglossans from three sites (Zanpa-misaki, Sobe, and Sunabe) on the southwestern coast of Okinawajima (Figure 1C).

Collections and experiments: Our specific field collections were as follows. In May 2000, we collected *Codium fragile* ssp. *fragile* (covered with epiphytes of the red alga *Polysiphonia* sp. and the sacoglossan *Stiliger berghi*) from ropes suspended within Moroiso Bay at MMBS. We examined the single egg mass produced by *S. berghi* in the laboratory (field-collected masses had already undergone several cell cleavages). We measured the maximum and minimum length of 10 uncleaved ova and capsules within the egg mass. When veliger larvae hatched from the spawn mass, we measured the maximum shell length of 10 veligers.

In July 2001, we collected >100 *Stiliger berghi* on free-living red algae in various areas on the eastern shore of Oshoro Bay, Hokkaido (Figure 1A). We conducted short-term feeding-preference experiments at the Oshoro Marine Station, Hokkaido University. We offered individual specimens of *S. berghi* pairwise choices of three algal hosts: *Dasya sessilis*, *Polysiphonia* sp., and *Ceramium* sp. We monitored the number of specimens on each alga periodically throughout a one-day period and compared slug choices with Pearson's

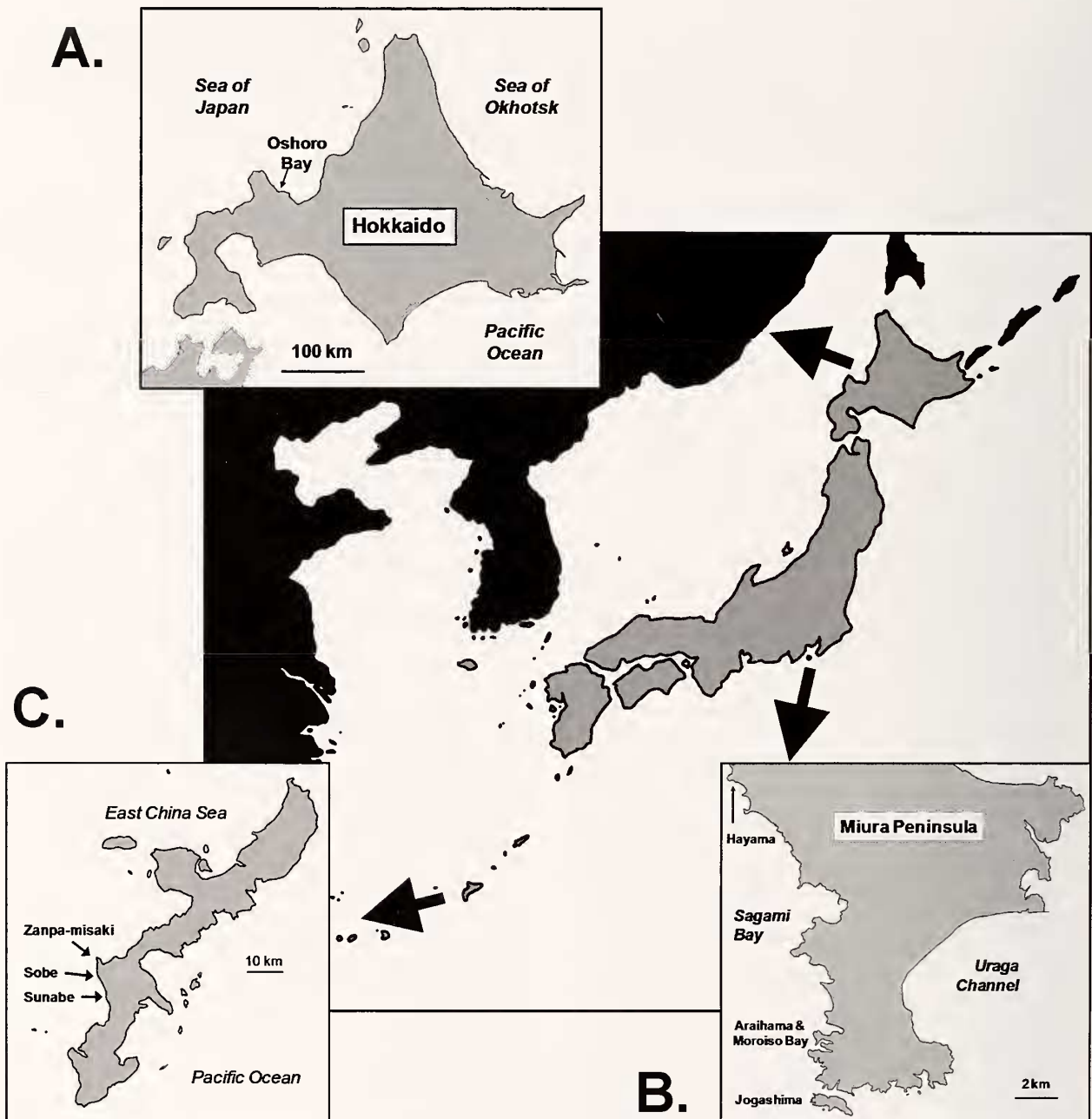


Figure 1. Map of three major study areas in Japan from north to south: (A) Oshoro Bay, Hokkaido; (B) Miura Peninsula, Honshu; and (C) Okinawajima, Okinawa.

chi-square test and Fisher's exact test on the categorical data.

In spring 2004, 2005, and 2006, we collected epiphytic and free-living *Polysiphonia* spp. from ropes suspended in Moroiso Bay. We also made collections of *Zostera* from Moroiso Bay (with red algal epiphytes) and ceramialean red algae from the adjacent rocky shore, Araiama, at MMBS.

In March 2004, we hatched veligers to remeasure shell length. Furthermore, we conducted another feeding experiment to determine whether *Stiliger berghi* exhibited feeding preferences for thalli of different life-history phases. Red algae belonging to Ceramiales typically have a complex life history with haploid female and male thalli (gametophytes) coexisting with morphologically similar diploid thalli (tetrasporo-

phytes). Herbivores that feed on these algae may exhibit preferences between the isomorphic haploid and diploid phases. In March 2004, we conducted a pairwise-choice experiment with female gametophytes and tetrasporophytes of *Polysiphonia harveyana*. Prof. Chris Maggs (Queens University, Belfast) kindly identified the species on morphological and molecular grounds. The logistical details were similar to those of the experiment above. In April 2008, we collected 8 specimens of *S. berghi* from *Polysiphonia (sensu lato)* spp. and 1 from *Ceramium* sp. on the floating docks at Hota on the eastern shore of Sagami Bay, Honshu. The specimens were held in separate small containers filled with seawater and offered the red alga *Griffithsia japonica*. Observations were made a few times a day for 6 days to evaluate whether the sacoglossan could consume *Griffithsia*.

Finally, we made seven visits to Okinawajima between July 2002 and April 2006. We collected ceramialean red algae primarily at Sunabe, Chatan, on the reef crest and at Zanpa-misaki on the reef platform. Smaller collections were also made in reef-crest and reef-lagoon areas of Sobe. Small, cryptic sacoglossans could not be observed directly on the shore. Therefore, specimens of *Elysia* sp. were sampled by collecting red algae, holding them in shallow trays with seawater for 1 to 2 days, and then hand-picking the slugs from the algal surfaces or the air-water surface. Because of the physical conditions (moderately wave-exposed habitats) and the ecological ones (intense herbivory), the red-algal thalli were typically <1 cm long and could be identified only to genus.

Specimens of *Elysia* sp. were held in the laboratory in containers with different algal genera. Because of low sample size, formal experiments were not conducted, but feeding damage on different algal genera was recorded when observed. The single egg mass produced in the laboratory was collected; the diameters of ova and capsules were measured.

RESULTS

Stiliger berghi

External features: The simple rhinophores of *Stiliger berghi* had a distinctive brown stripe encircling the upper end (Figure 2A–C). There was scattered purple-brown pigment on the epidermis on the dorsal surface; the sole of the foot was white although the pigment was present around the margin. This species had a very pronounced C-shaped, brownish-purple esophageal pouch (Figure 2B, C). The ingested red algal chloroplasts were visible in the digestive tract, particularly in specimens that had recently fed. There were two longitudinal tubes that extended branches into the cerata but not into the tail. The anus was small and dorso-anteriorly situated.

The species grew to 10 mm long and 11 mg in wet weight, but most specimens were much smaller (Figure 3A–C). Of 45 specimens examined in April 2006 (Figure 3D), *Stiliger berghi* had 4 to 11 cerata per side (mean = 15 cerata total, maximum = 21); however, some large specimens collected on 4 March 2004 had 15 cerata per side.

The species had pointed radular teeth with an unusual knob-like tip (Figure 4A–C). The ventral side of each tooth had a concavity, and the tip was blade-like with small denticulations on the central, keel-like edge. An extremely unusual feature was that the denticulations were on both the ventral and the dorsal edges of each tooth tip (Figure 4C). Based on 17 specimens (1–3 mm long) collected in July 2001 from Oshoro Bay, the number of ascending teeth varied from 6 to 8; the number of descending teeth varied from 17 to 23, including the three preradular teeth. The length of the leading tooth varied from 80 to 135 μm ; the base width varied from 25 to 40 μm . Our observations of tooth shape, size, and number are consistent with the species description, with two rather minor exceptions. (1) Baba (1937) mentioned the highly distinctive teeth were smooth, based on light microscopy; with currently available, high-resolution microscopy, the denticulation is readily apparent. (2) The original description states there were five teeth in the descending row and 19 teeth in the ascending row; we respectfully suggest that Baba inadvertently switched the terms *ascending* and *descending*.

Reproduction and development: *Stiliger berghi* copulated frequently in the laboratory. Slugs started by vigorously pressing the anterior part of the head together with that of a conspecific. The slugs then aligned themselves right eye to right eye. Copulation took several minutes and was reciprocal; the short penis lacked a stylet. The slugs copulated sequentially with many different slugs.

The egg masses of *S. berghi* were oval and were deposited among the branches of the polysiphonous red algae. The slightly oval ova averaged $62 \times 68 \mu\text{m}$ in diameter, and capsules were $104 \times 136 \mu\text{m}$. When veliger larvae hatched from the spawn mass in May 2000, initial shell length averaged 116 μm . In March 2004, recently hatched veligers averaged 114 μm in shell length ($n = 5$) and had type I shells (sensu Thompson, 1961).

Feeding ecology: We found several algal hosts and observed feeding activities of *Stiliger berghi*. In May 2000, some of the subtidal thalli of *Codium fragile* ssp. *fragile* that we collected from Moroiso Bay had the epiphytic red alga *Polysiphonia* sp. We found 33 individuals of *S. berghi* on five thalli of *C. fragile* with this epiphyte. Cell size of the epiphyte on the main axes was about 200 μm wide and 300–400 μm long; on

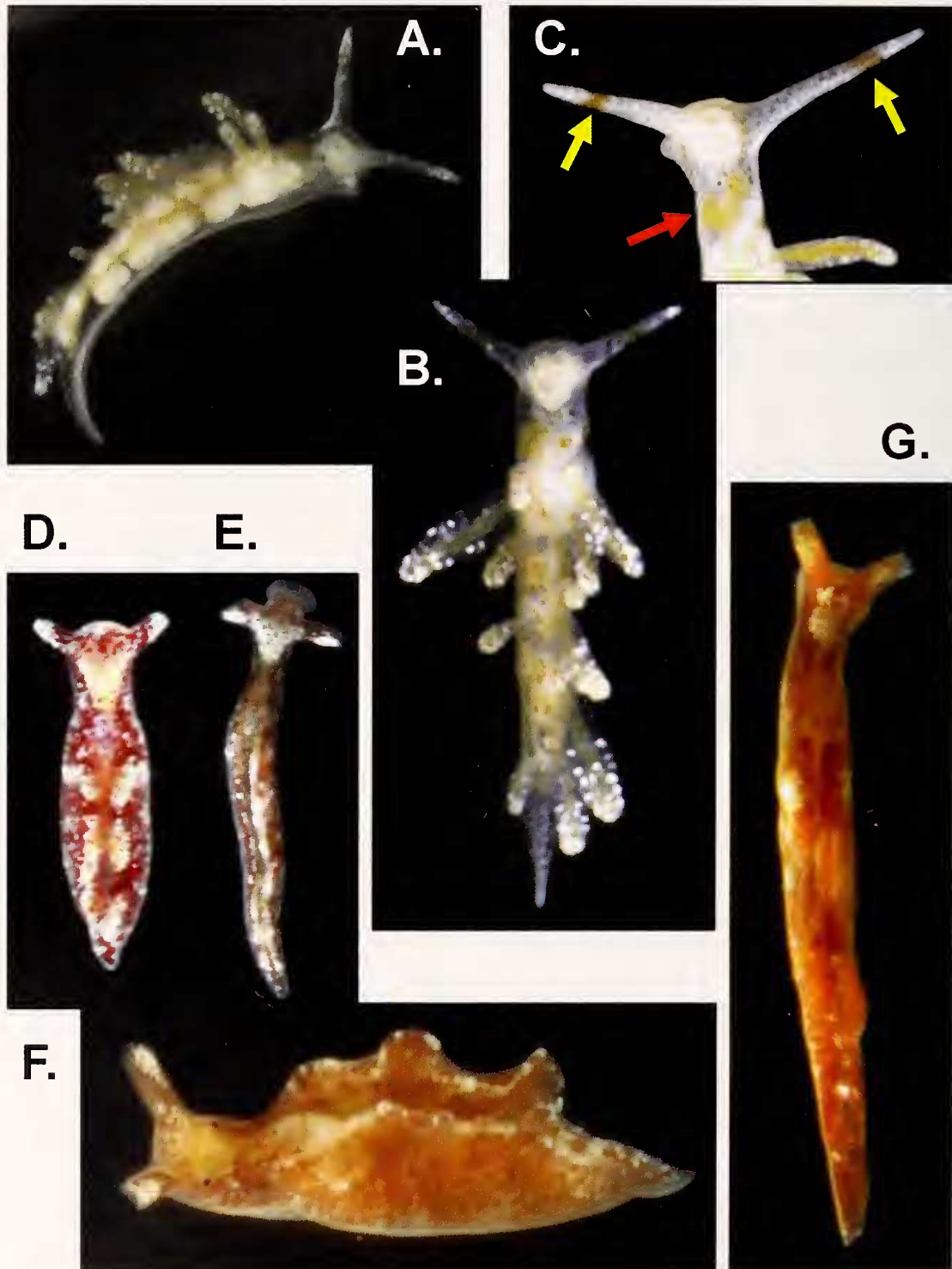


Figure 2. (A) Oblique right view, (B) dorsal view, and (C) close-up of head of a specimen of *Stiliger berghi* from Oshoro Bay, Hokkaido, Japan. Arrows indicate characteristic color bands on the rhinophores and the visually distinct esophageal pouch. (D–F) Dorsal and oblique views of *Elysia* sp. specimens from SW Okinawajima; (G) dorsal view of *Elysia* sp. from Shirahama, Shimoda, Honshu. Individuals ranged from 3 to 6 mm long.

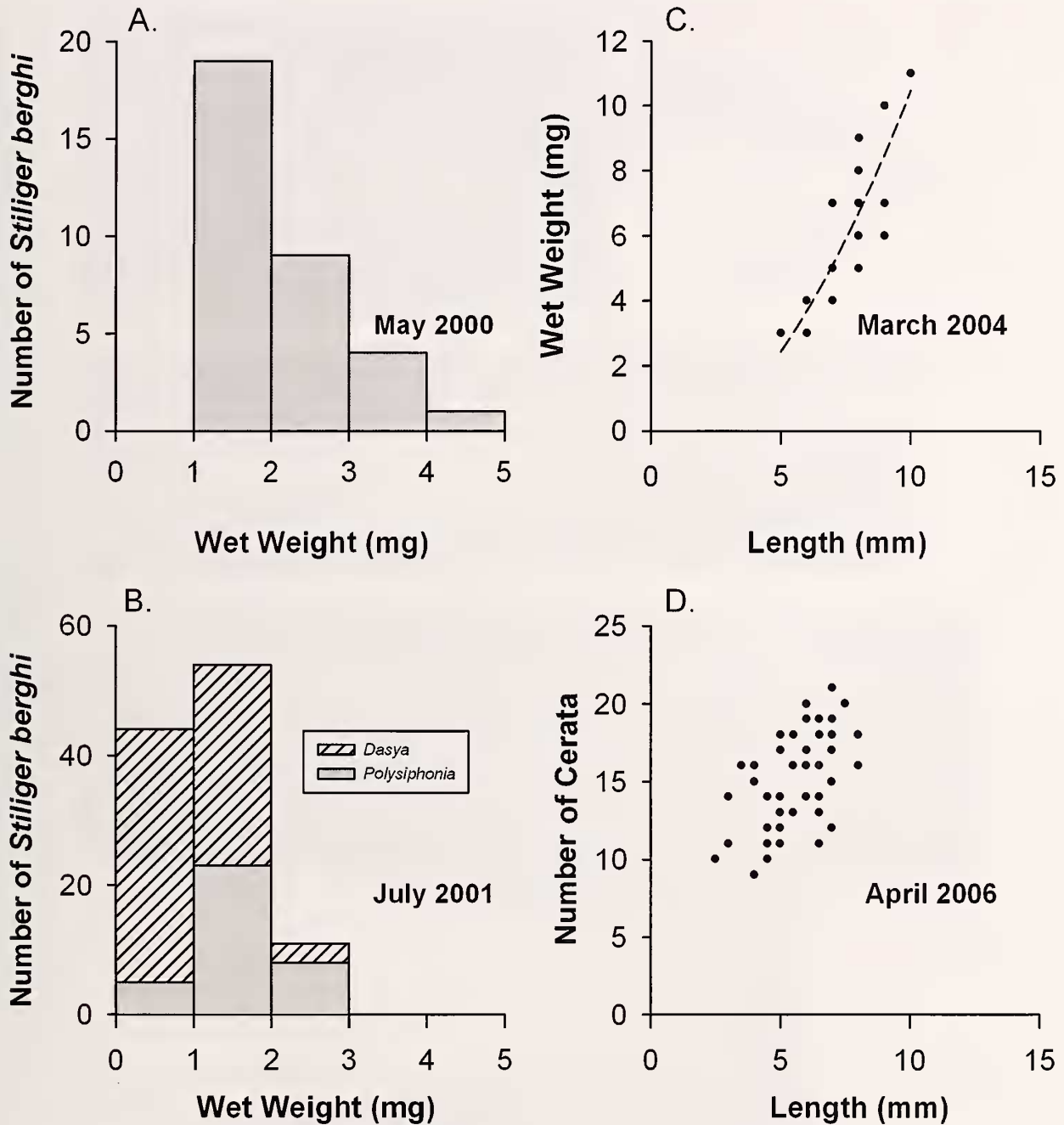


Figure 3. Body size of *Stiliger berghi* from (A) Sagami Bay in May 2000, (B) Hokkaido in July 2001, and (C, D) Sagami Bay in March 2004 and April 2006.

terminal branches, cell size ranged from 200 μm wide and 340 μm long to small terminal cells 40 μm wide and 40 μm long. Thus, a wide range of cell sizes was available on which slugs could feed.

In July 2001 at Oshoro Bay, Hokkaido, we found high densities of *Stiliger berghi* on polysiphonous red algae, primarily *Dasya sessilis* and secondarily on

Polysiphonia sp. (Figure 3B). Specimens on *Dasya* were not only more abundant but also significantly smaller than those on *Polysiphonia* (Student's *t*-test, $t = 4.7$, $P < 0.001$). The overall sacoglossan abundance was 0.86 slugs per gram (wet weight) of ceramialean algae. In feeding-preference experiments, *S. berghi* preferred *Dasya* to *Polysiphonia* and strongly preferred both

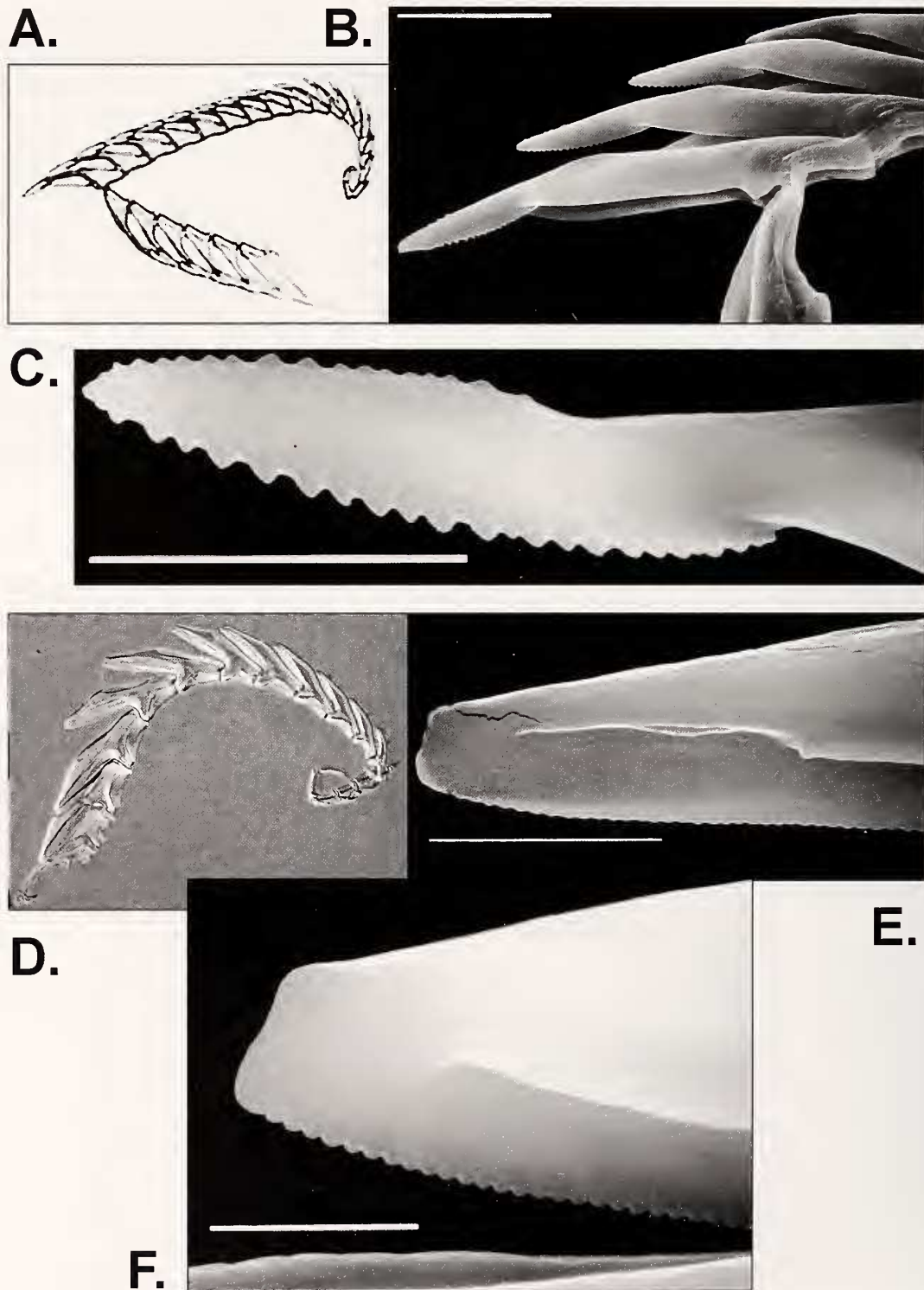


Figure 4. (A-C) Radula of a specimen of *Stiliger berghi* from Oshoro Bay, Hokkaido, Japan. (D) Radula of 2.5 mm *Elysia* sp. from SW Okinawajima. (E, F) Close-up of radular teeth of two specimens. Scale bars are (B) 50 µm, (C) 20 µm, (E) 10 µm, and (F) 5 µm.

Dasya and *Polysiphonia* to *Ceramium* (Figure 5). All of the initial preferences and two of the three final preferences were statistically significant (Pearson's chi-square tests, $P < 0.05$). We observed *S. berghi* feeding on all these red algae (even *Ceramium*): many cells were punctured and cytoplasm removed.

In March 2004, *Stiliger berghi* exhibited no preference between isomorphic female gametophytes (N) and tetrasporophytes ($2N$) of *Polysiphonia harveyana*. There was no significant initial or final difference in slug counts between algal life-history stages (Figure 6, Fisher's exact tests, $P = 1.0$ for both comparisons).

Finally, in April 2008, eight specimens of *Stiliger berghi* collected from *Polysiphonia* spp. were observed on the alga *Griffithsia japonica* in the single-choice trial. We confirmed feeding or attempting to feed in 3 of the 8 specimens. After 2 days, empty algal cells were observed in several containers.

Elysia sp.

External features: This species was an extremely small plakobranched with dense white spots on the rhinophores, dorsal surface of the neck, parapodial edges, and lateral surfaces (Figure 2D–F). The white spots were frequently most dense on the neck and in two patches on the parapodial edge. The red coloration varied among individuals from dark wine-colored to light orange-red, depending on feeding activities (algal host, time since last fed, etc.). The external surface was fairly smooth; there was no evidence of any distinct papillae. In November 2003, we found many individuals on red algae with the modal size of 3 mm (Figure 7). The maximum size we recorded at Okinawajima in seven visits from July 2002 to April 2006 was 6 mm.

The single specimen from Shirahama, Shimoda, on the Pacific coast of Honshu, was 8 mm. Although the rhinophores in this one specimen were spaced slightly closer than those in the Okinawan specimens shown (Figure 2), the spacing was within the morphological variation observed in all our specimens. Based on the similarity of the radular formula and highly distinctive tooth shape in the specimens, we consider the Honshu specimen to be conspecific with Okinawan specimens.

The radulae of *Elysia* sp. have 2–3 preradular elements, 10–17 descending teeth (excluding the preradular teeth), and 4–5 ascending teeth (including the forming “ghost teeth”) for five specimens examined of ca. 1.5 to 2.5 mm in preserved length (see Figure 4D, for example). The leading tooth varied in size: 54 to 69 μm in length and 14 to 19 μm in basal width. The teeth were blade-shaped with fine denticulation along the cutting edge (Figure 4E–F). One unusual feature, however, was the blunt tooth tip: it was almost

rectangular rather than the typical pointed form of most blade-shaped teeth of other sacoglossans.

Reproduction and development: The copulatory behavior of this species has not yet been observed, but we have recorded spawning in a 6-mm individual. Thus, this *Elysia* species attained reproductive maturity by at least 6 mm in body length. The egg mass was composed of tightly packed capsules with one embryo per capsule. There were small but distinct amounts of white extracapsular yolk distributed within the mass. Because multiple cleavages had already occurred, we were not able to determine ovum and capsule diameters of uncleaved ova. Based on our measurements of the existing spawn mass, the embryos were ca. 100 μm long and the capsules were ca. 200 μm in diameter.

Feeding ecology: The ceramialean red algae of Okinawa were extremely diverse, including most of the genera in Table 2; thus, we were not able to document fully all the algal hosts. However, *Elysia* sp. consumed red algae of several genera, including *Griffithsia*, *Wrangelia*, and *Polysiphonia*. Given the small size of these algae (<1 cm long) at our sites, we were not able to determine algal species.

DISCUSSION

Small size and cryptic appearance: *Stiliger berghi* and *Elysia* sp. are small species and extremely cryptic on their algal hosts. We predict that *S. berghi* is broadly distributed in central Japan during late winter to early spring, when *Polysiphonia* spp. and allies are lush. Specimens have been found in northern Japan only in summer: July collections in Oshoro Bay, Hokkaido (this report), and the 13 June 1997 collection in Noshappu, Wakkanai, on the northernmost part of Hokkaido (Y.J. Hirano & Y.M. Hirano, unpublished observations). The November 2003 peak of *Elysia* sp. was also suggestive of a winter species, but this could not be confirmed in subsequent years (Figure 7). We have found one specimen of *Elysia* sp. from Shirahama, Shimoda, on the Izu Peninsula of Honshu; the 8-mm individual (Figure 2D) occurred on red algal epiphytes (not identified) on *Codium latum* in July 2003. Although the Honshu specimen had minor external differences from those collected in Okinawa, we consider that the specimens are conspecific, based on the external morphology and distinctive shape of the radular teeth. If specimens of red *Elysia* of Ono (2004), Nakano (2004), and T.M. Gosliner (personal communication) are conspecific with ours, then this species may be broadly distributed in warm-water regions of Japan, the Philippines, and other NW Pacific and Indo-Pacific locations; otherwise, there may be a complex of *Elysia* species that feed on red algae.

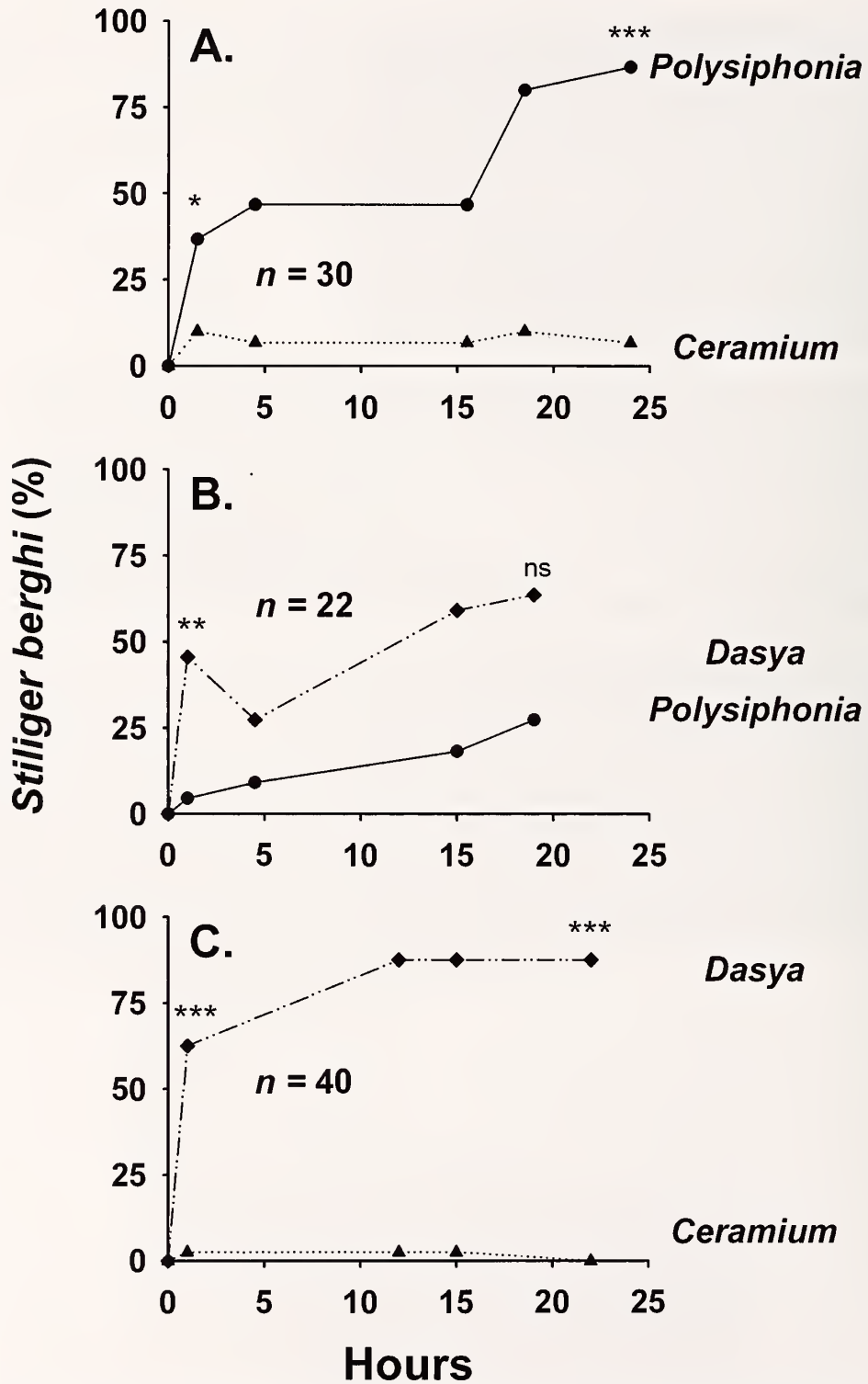


Figure 5. Feeding preferences of *Stiliger berghi* from Oshoro Bay, Hokkaido in pairwise-choice experiments with three sympatric, polysiphonous red algal genera. Data were collected in July 2001. The symbols are as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not statistically significant; n , the number of replicate slugs.

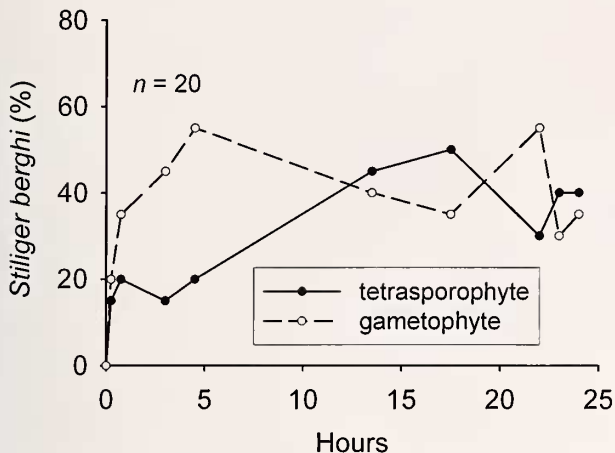


Figure 6. Feeding preferences of *Stiliger berghi* from Sagami Bay, Honshu when offered different algal life-history phases: haploid female gametophytes versus diploid tetrasporophytes of *Polysiphonia harveyana*. The experiment was conducted in March 2004.

Given that many species of Indo-Pacific *Elysia* species feed either on red algae or both red and green algae, how does our *Elysia* sp. differ? *Elysia furvacauda*, *E. abeilamakusana*, and *E. japonica* (sensu Jensen) all have black-tipped rhinophores and tail (Table 3); our species does not. Furthermore, the general body coloration of *Elysia* sp. does not correspond with that of any other superficially similar species, particularly those with orange, red, blue, or yellow spots scattered across the body (Table 3). In terms of internal anatomy (Table 3), Jensen (1985) reported that the radular teeth of *E. japonica* and *E. verrucosa* are almost identical (blunt, bladlike teeth) and that Baba (1955) considered *E. abei* and *E. japonica* teeth to be similar. However, the blunt, bladlike shape of these species is markedly different from the squared off, almost truncated shape of the specimens of *Elysia* sp. examined in this study. After investigating all published drawings and SEMs of *Elysia* radular teeth (worldwide), we consider the teeth of Japanese *Elysia* sp. to be distinctively different. Furthermore, our species does not correspond in coloration, external morphology, or algal hosts to the insufficiently described Okinawan *E. flavipunctata* Ichikawa, 1993, or *Elysiobranchus ryukyuensis* Ichikawa, 1993.

Not only are our two Japanese red-algal feeders underreported, but most of their ecological analogs around the world are underreported as well (Table 1). Most of these sacoglossans listed are a few mm long, except for *Hermaea variopicta* (as *Hermaeopsis*), *H. oliviae*, *H. wrangeliae* (both as *Aplysiopsis*), *Elysia abeilamakusana*, and *E. viridis*. The highly branched, delicate ceramialean algae render the red-algal feeders particularly visually cryptic. Many other sacoglossans with dietary homochrony (color derived from algal

food, resulting in excellent crypsis) are more apparent than the red-algal feeders because of the architecture of the algal hosts. For example, sacoglossans on planar algae (e.g., crustose *Codium*) or coarsely branched species (e.g., *Halimeda*, *Codium fragile*) often are comparatively easy to search for. The darkly pigmented sacoglossans that feed on bright green algae *Cladophora* and *Chaetomorpha* (e.g., see species of *Aplysiopsis* Deshayes, 1864, *Limapontia* Johnston, 1836, and *Ercolania* Trinchese, 1872) are considerably more apparent than sacoglossans on the uniseriate or polysiphonous filaments of red algae.

High densities and local distributions: The abundance and phenology of red-algal feeders is difficult to assess. *Hermaea bifida* and *Stiliger fuscovittatus* are considered to be frequent to abundant (e.g., Case, 1972), but most of their ecological analogs are considered to be sparse to rare. If attention were focused specifically on the algal hosts and sacoglossans were expressed on a per hostbasis (number of individuals per gram of host, per algal thallus, or per square meter of algal turf), these cryptic species may be locally quite abundant. Until malacologists standardize abundance values of sacoglossans by the abundance of algal hosts, we will have an incomplete understanding of their occurrence and potential community effects.

In Hokkaido, *Stiliger berghi* was reliably found on ceramialean algae on wave-sheltered shores; preliminary abundance values were 0.86 slugs per gram of host algae (wet weight). In San Francisco Bay, California, *S. fuscovittatus* occurred on average as 0.48 specimens per ml of *Polysiphonia pacifica* (wet weight), 2.69 per ml of *P. brodiaei*, and 0.57 per ml of *P. paniculata* (Case, 1972). On an area basis, *S. fuscovittatus* had a maximum local density of 177 specimens per square meter (Case, 1972). Comparable quantitative information is needed for other red algal feeders. In our study and in that of Case (1972), estimates of population density were determined on a wet-weight basis, not the dry-weight basis used by workers in the Atlantic. Thus, until all the wet-weight to dry-weight ratios have been calculated for all the Japanese hosts, Pacific red-algal feeders cannot be compared with NW Atlantic studies on green algal feeders; however, we do have quantitative abundance estimates for >10 Japanese sacoglossan species on green algae (Trowbridge, Hirano, & Hirano, unpublished data).

Stiliger berghi and its algal hosts have been recorded in several bays and harbors in close proximity to vectors of introduction (ship hulls and oysters). Its salinity tolerances and those of the ecological equivalent species around the world are largely unknown. A notable exception is the NE Pacific *Stiliger fuscovittatus*: Case (1972) reported that the species tolerated salinities ranging from 21 to 33 psu (practical salinity

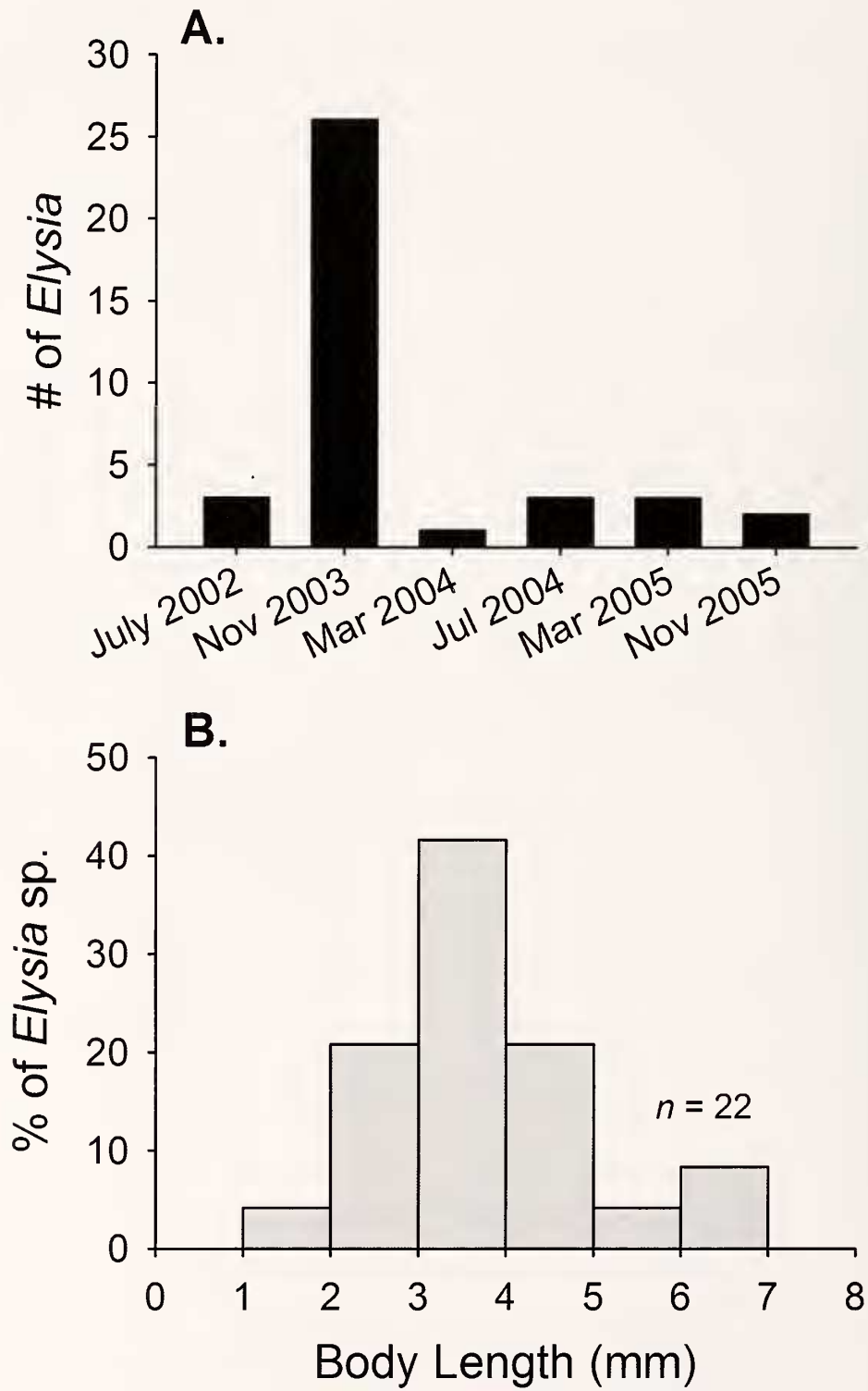


Figure 7. (A) Specimens of *Elysia* sp. collected from SW Okinawajima from 2002–2005. (B) Size-frequency distribution of the species in November 2003.

Table 3

Comparison of Indo-Pacific and western Pacific *Elysia* species that feed on red algae or are morphologically similar to those species. Details based primarily from Baba (1949, 1955), Brandley (1984), Jensen (1985), Ichikawa (1993), and this study.

<i>Elysia</i> species	Body coloration	Radular tooth shape	Radular teeth (counts and size)	Known algal hosts
<i>E. cf. furvacauda</i>	Reddish brown Black-tipped rhinophores Black-tipped tail	Tentatively: blunt tipped and denticulate	Not described	<i>Codium</i> <i>Microdictyon</i> Red algae
<i>E. abet / amakusana</i>	Black-tipped rhinophores Black-tipped tail Small orange-red dots across body	Denticulate bladeliike teeth	Leading tooth 173 µm long Six ascending teeth, 11–13 descending ones, and heap of teeth in ascus	<i>Bryopsis</i> <i>Chaetomorpha</i> <i>Cladophora</i> <i>Griffithsia</i> <i>Chaetomorpha</i>
<i>E. japonica</i>	Three color varieties (green, red, brown) Zigzag pattern of white or tan on parapodial margins Small yellow, orange, and blue dots across body Top of head and dorsal side of rhinophores white due to lack of diverticula Body grayish green Blunt papillae on head and parapodia	Smooth, bladeliike teeth	Leading tooth 173 µm long Six ascending teeth, 11 descending ones, and heap of teeth in ascus	
<i>E. verrucosa</i>	Black, orange, and red spots Rhinophores not black-tipped Tail not black-tipped Dark or light green Margins of parapodia white or dotted white Yellow spots across body Long, tapering rhinophores Three transverse stripes on rhinophores	Blunt, bladeliike teeth	Leading tooth 140 µm long Six ascending teeth, 9 descending ones, and heap in ascus	<i>Cladophora</i> <i>Chaetomorpha</i>
<i>E. flavipunctata</i>	Reddish brown Whitish spots concentrated on rhinophores, dorsal surface of head, edge of parapodia, and scattered over body Rhinophores not black-tipped Tail not black-tipped No brightly colored spots	Not described	Not described	<i>Halimeda</i>
<i>Elysia</i> sp. of this study		Blunt, bladeliike teeth Tip of blade squared off, distinctly different from <i>E. japonica</i> and <i>E. verrucosa</i>	Leading tooth 54–69 µm long 4–5 ascending, 10–17 descending ones, and 2–3 pre-radular elements	Monosiphonous red algae Polysiphonous red algae

units). The LD₅₀ values (lethal dose for 50% of specimens) for *S. fuscovittatus* at 10 and 13 psu were 18 h and 72 h, respectively. Thus, this NE Pacific species could survive in estuaries and bays, predisposing it to be inadvertently introduced to other regions (probably accounting for reports from Florida and the Gulf of Mexico). The only other salinity estimate that we have found is 16 psu at the site where *Hermaea cruciata* was collected in the Atlantic (Vogel, 1971; Marcus, 1972).

Reproduction and development: Baba & Hamatani (1952) illustrated and briefly described the spawn mass of *Stiliger berghi*: the shape (oval), size (max. 4 mm long × 1 mm broad), and coloration (ova were unpigmented). Our results were consistent with their description. Furthermore, our ovum and capsule-size values for *S. berghi* (Table 1) were consistent with those of Hamatani (1960, 1963). Although not quite as small as those recorded for *H. bifida*, the ova of *S. berghi* are among the smaller ones recorded for sacoglossans (Clark & Jensen, 1981; Jensen, 2001). The ovum, capsule, and shell sizes indicate that *S. berghi* probably has planktotrophic larvae; the type I shell also supports this inference.

Our results with the egg mass of *Elysia* sp. cannot be well compared with the egg masses of other sacoglossans, given that we had a single spawn mass and that several embryonic cleavages had already occurred. There were two notable points, however: (1) There was white extracapsular yolk distributed within the mass, comparable with that seen in many other *Elysia* spp. (Jensen, 2001; Patrick Krug, personal communication). (2) The embryos were relatively small (ca. 100 μm), suggestive of planktotrophic larvae (but see Clark & Jensen, 1981; Jensen, 2001).

Long-lived planktotrophic larvae (of any invertebrate) produced within bays, particularly those with commercial shipping, have a greater probability of dispersal via ballast-water uptake and discharge than do short-lived, lecithotrophic larvae or the larvae of open-coast species. Thus, the wave-sheltered habitat, coupled with the long planktonic period of most sacoglossans (typically weeks to months), may predispose these species to being introduced accidentally via international trade. The major vector for introduction and movement of ceramialean algae is hull fouling (reviewed by Trowbridge, 2006); thus, sacoglossans that settle on red algae on a ship hull may be unintentionally dispersed within or between ocean basins, depending on the sacoglossans' tolerance for water currents past the hull and for variations in water temperature and salinity in different embayments. After an initial introduction, species with planktotrophic larvae would have a greater probability of marginal dispersal via coastal currents or other

mechanisms than species with short-lived larvae or with direct development. Thus, red-algal feeders with planktotrophic larvae that dwell in bays may not be as locally endemic as initial reports imply. However, there are internationally supported criteria for recognizing introduced species (reviewed by Trowbridge, 2006) that need to be explicitly considered in evaluating any purported introductions.

Feeding ecology: The diet breadth of Japanese red-algal feeders is difficult to evaluate. Baba (1937) recorded the Japanese *Stiliger berghi* on *Zostera* weeds (presumably on red-algal epiphytes) and on the red algae *Ceramium*, *Polysiphonia*, and *Galaxaura* (Baba, 1959). However, Baba did not report actual feeding observations but rather field associations, which may or may not reflect trophic associations. *Polysiphonia* spp. (*sensu lato*) are frequently sacoglossan hosts, and *Ceramium* spp. are occasionally hosts. However, *Galaxaura* is a calcified red alga and probably not consumed by *S. berghi*. In fact, we have often observed thin strands of green and red filamentous algae among the calcified branches that may well be sacoglossan foods. Thus, we know that *S. berghi* feeds on at least four of ten genera of ceramialean red algae known to be sacoglossan hosts (Table 2).

The subtropical to tropical *Elysia* sp. has been collected from, and fed on, several algal hosts (this study). The small size (<1 cm) of the intertidal host algae in Okinawajima constrained detailed investigations. Hopefully, future subtidal studies in Japan and SE Asia will elucidate the species' seasonality and algal-host associations. What is particularly intriguing is that the teeth of *Elysia* sp. are fundamentally different from those of its ecological counterpart on temperate to boreal shores—namely, *Stiliger berghi* (Figure 4A–F)—and from all other red-algal feeders worldwide.

Sacoglossan species consume red algae on most shores throughout the world. Their feeding habits and diet breadth are extremely difficult to characterize, owing primarily to the taxonomic challenges posed by the algal hosts and secondarily to the insufficiency of published literature on the subject. The two seemingly well-characterized NE Atlantic sacoglossans exemplify this problem: *Hermaea bifida* and *Elysia viridis* (Table 1).

Thompson (1976) reported that *H. bifida* “was usually found on red algae, such as *Griffithsia*, *Delesseria*, and *Heterosiphonia*” (p. 174). Garstang (1890) recorded the sacoglossan “creeping over a frond” of *Delesseria hypoglossum* and stated that the slug would not eat the alga during a 12-day experiment. Yet, *Delesseria* has persisted as a presumed host in the literature. Other major hosts were not listed—*Halurus* (e.g., *H. equisetifolius*) recorded by Duerden (1896) and *Bornetia* (e.g., *B. secundiflora*) recorded by Cornet &

Marche-Marchad (1951) and cited by Miller (1958). *Hermaea bifida* has been reliably reported from five genera of algae (Table 1), yet the sacoglossan review by Williams & Walker (1999) reported only a single genus (*Griffithsia*) and the review by Händeler & Wägele (2007) reported four genera.

The literature on *Elysia viridis* illustrates a comparable underestimate. Thompson (1976) reported a number of algae, but many of those listed do not represent algal foods. Typically cited hosts include *Codium*, *Bryopsis*, *Cladophora*, and *Chaetomorpha* (Williams & Walker, 1999; Händeler & Wägele, 2007). Yet red-colored *E. viridis* and the capacity to consume red algae have been known for over a century (Garstang, 1890; Thompson, 1976, and references therein). The sacoglossan feeds on at least four genera of red algae: *Griffithsia*, *Halurus*, *Dasya*, and *Dasyisiphonia* (Van Bragt, 2004; Trowbridge, personal observations). Consequently, *E. viridis* feeds on at least eight genera, including green and red algae, native and introduced.

With a thorough consideration of the primary literature and enhanced field investigations, we may all improve our estimates of the breadth of the sacoglossan diet. The fact that *Hermaea bifida* and *Elysia viridis* have at least five to eight algal genera as hosts is cautionary to proponents of the notion that the breadth of the diet of sacoglossans is narrow. Sacoglossans can and do change algal hosts on spatial and temporal scales (Trowbridge & Todd, 2001; Trowbridge, 2004).

Sacoglossans that feed on filamentous algae (green or red) tend to fragment the hosts. With uniseriate green or red filaments (e.g., *Cladophora* and *Chaetomorpha* versus *Griffithsia* and *Halurus*), the removal of cytoplasm from a cell can cause structural damage to the alga, resulting in fragmentation. Polysiphonous algae may be slightly more robust, but herbivore-induced damage in wave action contributes to the removal of substantially more algal biomass than the amount consumed (Trowbridge, 1993). Ceramialean algae have a great propensity for their fragments to regenerate and/or reattach. Therefore, sacoglossan herbivory may enhance or exacerbate the spread of introduced red algae in a manner similar to that described for the sacoglossan *Lobiger serradifalci* (Calcara, 1840) feeding on *Caulerpa taxifolia* in the Mediterranean Sea (Žuljević et al., 2001).

Kleptoplasty: Of the 20 species of red algal feeders (Table 1), only a few have been evaluated for the functionality of their ingested algal chloroplasts. (1) *Hermaea bifida* had long-term functional chloroplast retention (Taylor, 1971; Kremer & Schmitz, 1976; Kremer, 1977). (2) The congener *H. cruciata* exhibited medium-term, nonfunctional retention (Clark et al.,

1990). (3) The survival of starved *Stiliger fuscovittatus* held in the light versus dark was investigated by Case (1972), but the results were inconclusive. (4) *Elysia* cf. *furvacauda* retained functional chloroplasts of both red algae and green algae seasonally (Brandley, 1984) in an intriguing study of seasonal host shift. (5) Finally, there have been extensive studies with *Elysia viridis* on the species' long-term, functional retention of chloroplasts of the introduced green alga *Codium fragile* ssp. *fragile* (previously called *C.f.* ssp. *tomentosoides*), which have been (reviewed by Williams & Walker, 1999; Trowbridge & Todd, 2001). However, the capacity to retain chloroplasts of the native green algae *Codium vermilara* and *C. tomentosum* (*sensu stricto*) is unclear because the algal hosts were misidentified in many of the classic papers on kleptoplasty of *E. viridis*; furthermore, the species' capacity to retain red algal chloroplasts has never been investigated, although the species readily consumed four red algal genera (Table 1).

What is the probability that *Stiliger berghii* and/or *Elysia* sp. have functional kleptoplasty? Past studies indicate that some of the red-algal hosts have chloroplasts sufficiently robust to maintain functional kleptoplasty. Furthermore, several related sacoglossans have functional kleptoplasty. However, functional kleptoplasty may have evolved multiple times. The assemblage of red-algal feeders needs to be investigated before generalizations can be made.

Prospectus: The ecology of sacoglossans that feed either selectively or partially on ceramialean red algae has been understudied, compared with species that feed on green algae. We suggest that there are several priority areas for future research:

1. There is a need to characterize more fully the sacoglossan species that feed on red algae, particularly confirming generic affinity on morphological, reproductive, and molecular bases.
2. Future investigators should describe the algal hosts of sacoglossans to genus level (at least) so that diet breadth can be examined more objectively. Feeding experiments should be conducted to confirm actual feeding damage and to determine host and nonhost red algae, particularly introduced versus native red-algal hosts. Also, collection and preservation of algal vouchers and their deposition in herbaria would facilitate better future identification of algal hosts.
3. Sacoglossan research is needed at the population level, quantifying the extent of herbivory, based on feeding rates, population abundances, and degree of functional kleptoplasty.
4. The distribution and salinity tolerance of these red-algal feeders need to be documented more fully so the proximity to potential vectors of introduction and the risk of spread (intraocean,

transocean, and interocean) can be evaluated. With the accelerating frequency of introductions, malacologists should consider whether local species are indeed native or have arrived from distant shores. Internationally recognized criteria should be used to assess the status of introduced species.

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